

ART. VIII. A NEW GOPHER FROG FROM THE GULF COAST,
WITH COMMENTS UPON THE *RANA AREOLATA* GROUP

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(PLATE XII)

A study of Florida amphibians has shown that the Gopher Frog which inhabits extreme eastern Louisiana and southern Mississippi is sharply distinct from *Rana capito* Le Conte, the Gopher Frog of Florida, Georgia, and the Carolinas, and equally distinct from *Rana areolata* Baird and Girard, the Crayfish Frog, which ranges from Texas to Indiana. Although well represented in various collections, this frog has remained undescribed principally because there are no examples of it in the United States National Museum collection, which includes the types of *areolata*, *aesopus*, and *capito*. A worker as careful as Francis Harper would not have overlooked this frog when he synonymized *aesopus* with *capito* (Harper, 1935) if specimens of it had been at hand for comparison with the several types.

The new species, with a wartier and more heavily pitted dorsum than any other North American *Rana*, probably secretes large quantities of mucus, and may, therefore, be called

Rana sevosa¹, new species

(Plate XII)

DARK GOPHER FROG

1922. *Rana areolata* Löding (not of Baird and Girard), Alabama Mus. Nat. Hist., paper no. 5:19.
1931. ?*Rana aesopus* Viosca (not of Cope), Southern Biol. Supply Co., Price List no. 20—Herpetology: 7.
1932. *Rana aesopus* Allen (not of Cope), Amer. Mus. Novitates, no. 542: 9.
1938. *Rana areolata* Burt (not of Baird and Girard), Trans. Kansas Acad. Sci., 41: 349 (part).

Type.—Carnegie Museum No. 16809, adult male, collected at Slidell, Saint Tammany Parish, Louisiana, April 11, 1926, by Percy Viosca, Jr.

¹Medieval Latin *sevosa* (slimy, tallowy) from classical Latin *sebosa* (tallowy).



Paratypes.—Fifty, all from Mississippi, as follows: CM 4944, CM 18116-18117, CM 18184-18197, from Van Cleave, Jackson County; MZUM 76921 (9 specimens) and MZUM 71777 (2 specimens) from Vestry, Jackson County; FMNH 11511-11514 and MCZ 15803-15806 from Jackson County; AMNH A37089-37099 and FMNH 21610 from Biloxi, Harrison County; and CM 5407-5408 from near Biloxi, Harrison County.

Diagnosis.—A dark, medium-sized *Rana* with a very warty dorsum and a heavily spotted venter. Its dorsal spots are frequently indiscernible from the dark ground color, but when distinct they are irregular in shape and are not outlined with a light color. *Rana sevosa* can be distinguished from both races of *areolata* by its spotted venter, lack of circular, light-bordered dorsal spots, warty dorsum with broad dorsolateral folds, and broad head. *Rana sevosa* differs from *capito* in having a darker ground color, heavier and more extensive ventral markings, broader waist, narrower dorsolateral folds, wartier dorsum, and dark hind limb bars which are broader than the light spaces between the bars.

Description of type.—Form moderate; body depressed; limbs short and stout; head broad posteriorly and tapering rapidly to snout, triangular in outline from above, moderate in profile, and with the dorsal surface slightly depressed; muzzle subacuminate; snout protruding beyond lower jaw; a small, indistinct, semicircular vocal sac behind the angle of the jaw and below the postlabial fold on each side of the head.

External nares halfway between eye and tip of snout, slightly below canthus rostralis; internarial distance greater than interorbital distance; canthus prominent; loreal region concave; eyes medium-sized, slightly longer than their distance from the nares; tympanic membrane nearly round, separated from the eye by about two-thirds of its own diameter, which is in turn about two-thirds the diameter of the eye; angle of jaws extending to below rear of tympanum, separated from it by about one-half the diameter of the latter; tympanum partly encircled posteriorly by a narrow groove which extends from posterior margin of eye to above axilla; this groove is overlapped by a heavy diagonal post-tympanic fold that leaves the dorsolateral fold immediately above the tympanum and extends obliquely downward to the postlabial fold on left side of head but fails to reach this fold on right side; the upper jaw becomes increasingly swollen posteriorly and gives rise to a broad, longitudinal postlabial fold that terminates at a point above the posterior insertion of the forelimb.

Dorsolateral folds, broader than high and heavily pitted, originate on the canthus rostralis slightly anterior to the nares, diverge backwards and cover the entire median halves of the upper eyelids; then curve sharply outwards immediately behind the eyelids, expand greatly at the points of junction with the post-tympanic folds, and extend backward as broad folds

(occasionally broken by deep, narrow, transverse creases) to the posterior third of the body.

Entire dorsum (between dorsolateral folds) and sides—but not top of head—studded with numerous, rounded, elongate, glandular warts, which are similar to the dorsolateral folds in texture; most of the dorsal warts twice as long as broad and some fused to form short folds; lateral warts round or slightly elongate but more widely spaced and invariably separate; top of head and spaces between warts finely pustular.

Ventral surfaces of body and limbs smooth except for femora and posterior part of belly, which are very slightly granular; no subgular fold present; a conspicuous interaxillary fold of skin on breast; from interaxillary fold on each side an oblique fold extends towards, but does not reach, angle of jaw.

Forelegs short, rather heavy, skin of body extending out only slightly on humerus; free portion of upper arm shorter and more slender than forearm; hand longer than forearm; palm with one large, rounded tubercle at base of central digits, a smaller elongate tubercle at base of fourth, and an indistinct, rounded tubercle above base of thumb; subarticular tubercles prominent; fingers four, stout, not webbed at base, not dilated at tips—third longest, first shorter, fourth and second nearly equal; thumb slightly swollen, with pale gray nuptial pad.

Hindlegs medium length, stout; tibio-tarsal articulations overlap slightly when femora are at right angles to body; tibio-tarsal articulations reach orbits when legs are adpressed; a transverse fold of skin across knee, another across heel, a rather indistinct tarsal crease; a narrow, longitudinal fold on upper surface of tibia; a distinct tarsal fold from fold of skin across heel to base of inner metatarsal tubercle; a short, indistinct fold along outer edge of tarsus; tibia slightly longer than femur; tarsus slightly more than one-third the length of whole foot; two metatarsal tubercles, the inner larger, elongate, and about one-third the length of first toe, the outer small and rounded; subarticular tubercles distinct; toes slender, not dilated at tips—4-3-5-2-1 in order of decreasing length, the third reaching to middle of the antepenultimate phalanx of the fourth; toes fully webbed to proximal half of antepenultimate phalanx of fourth, penultimate of third and fifth, ultimate articulation of first and second; ultimate phalanx of each toe completely free of web; toes three, four, and five margined to ultimate articulation.

Tongue large, obovate, greatest width slightly less than half that of mouth at angles of jaws, widest just posterior to center; anterior two-thirds broadly attached; two short horns on posterior margin indented from posterior corners and separated by median notch; internal nares sub-circular, well forward; maxillary teeth small, distributed along whole length of jaw; vomerine teeth small, few in number, on two oval clumps between internal nares from which they are separated by the width of a naris; widest apart anteriorly and almost in contact posteriorly.

Coloration of type (preserved).—Ground color above buff gray, changing

to ash gray on sides; the former color largely, and the latter partially, concealed by numerous dark brown, irregular spots; spots largest on central portion of back and generally extending on each side of oval dorsal warts, superimposed on dorsolateral folds, usually co-extensive with rounded lateral warts; spots bordered only by adjacent ground color and without light centers. Lower half of upper lip, loreal, and postocular regions buff gray with small fuscous markings; upper portion of upper lips and also top of head with irregular, dark brown spots; tympanum with asymmetrical light gray blotch surrounded by, and partially overlaid with, small brown spots. Forelegs with four or five short, dark bars; femur, tibia, and tarsus crossed by about four heavy, dark brown bars, separated by narrow interspaces of ash gray; distinct brown bands on toes four and five; small pale spots on toes one to three; concealed surface of tarsus heavily spotted; rear surfaces of thighs with large black blotches separated by gray interspaces. Entire ventral surface buff, all except central portions of thighs thickly sprinkled with fuzzy gray markings, largest on distal halves of thighs.

Measurements of type (in millimeters).—Snout-to-vent length, 82.5; head length (snout to posterior edge of tympanum), 28.5; head width (at posterior angles of jaws), 35; snout to naris, 7; naris to eye, 6.5; internarial distance, 6.5; interocular distance, 5.5; length of eye, 8; diameter of tympanum, 6; forearm, 18.5; hand, 20; longest finger, 15; femur, 36.5; tibia, 37.5; tarsus, 22; whole foot, 60; fourth toe, 38; interolecranal extent (distance between elbows when humeri are extended in the same line at right angles to longitudinal axis of body), 59.5; intergenual extent (distance between knees when femora are extended in the same line at right angles to longitudinal axis of body), 69; tongue length on median line, 18.5; length of horn, 3; tongue width, 15; interior internarial distance, 9; distance between ostia pharyngea, 22.5; distance from internal nares to ostia pharyngea, 14.

Variation.—The numerous paratypes of *sevosa* are remarkably uniform in all important characters. The one that shows the greatest variation, namely, the prominence of the dorsal warts, probably reflects differences in preservation rather than significant variation in nature. Dorsal warts are always present, numerous, and readily visible, but they vary considerably in elevation and in shape; some are circular, some are elongate-oval, and some are long ridges. The wartiest specimens are without any areas of smooth skin on the sides or back, the large warts being separated by a pebbling of fine granules and small warts. The large warts, the secondary warts, and the various folds are heavily and uniformly pitted.

The dorsolateral folds begin at the nostrils, extend backwards over the upper eyelids, and terminate at a point opposite the sacral hump, or extend beyond this point halfway to the hind limbs. A glandular ridge extends from the coccyx forward to about the presacral articulation, on each side of

the mid-dorsal line, in some specimens. A narrow, longitudinal tibial fold of variable length is visible in the more rugose specimens, and short, accessory folds or rows of warts may occur. Two tarsal folds are normally present, but these are difficult to see in soft specimens.

The fingers are usually 3-1-4-2 in order of decreasing length but occasionally 3-4-2-1 or 3-1-2-4. The toes are normally 4-3-5-2-1, but one specimen has 4-5-3-2-1 on one side. The webbing on the fourth toe is usually broadly attached at, or beyond, the antepenultimate articulation and extends forward as a margin of decreasing width to the ultimate; in one specimen it is broadly attached at the penultimate. The vomerine patches are not in contact in any specimen, but they vary from very slight separation to separation equalling their short diameter.

In dorsal coloration the paratypes range from an almost uniform black to a pale gray or light brown ground color with superimposed reddish brown or dark brown spots. None of the specimens is as light in ground color as *capito*, and none has dorsal spots encircled with light borders as in *areolata*. The venter is invariably thickly spotted anteriorly, but the spots, which lack sharp edges, vary in shape from amoeboid or vermiculate to mere concentrations of fine stippling and range from light gray or brown to red-brown in color. They are superimposed on a dirty white or tan background, which may be finely stippled with gray. The chin, throat, and pectoral areas are always spotted; the posterior portion of the belly and the central lower surfaces of the thighs are usually well-spotted in males and immaculate or lightly marked in females.

The femur, tibia, and tarsus are usually crossed with dark bars, but in a few specimens these are distinct only upon the anterior face of the femur. The bars vary in width, and the gray or brown interspaces that separate them range from very narrow to almost the width of the bars. When the interspaces are broad they may contain irregular dark spots or short lenticular interbars. The concealed surface of the tarsus is invariably well-spotted.

Secondary sexual characters.—No sexual differences in general body form have been observed. Variations in relative head length, head width, tibial length, and tympanic size appear to be individual rather than sexual. The forelegs of adult males are moderately enlarged. A nuptial pad, uniform gray in color, is present on the inner side of the first finger of all males except the three smallest specimens. The external vocal sacs, consisting of loose folds of dark skin above the forearm, may be hard to distinguish in preserved specimens; in undetermined specimens, slitting the

skin in this region is usually sufficient to demonstrate the presence or absence of the subdermal vocal pouch. The feet of males are somewhat more extensively webbed than are those of females. In the series examined, the males average much darker above than the females, but this distinction may not hold good with living material. The posterior portion of the belly, the inner surfaces of the forearms, and the central inferior thigh surfaces are normally well-spotted in males and immaculate or lightly spotted in females. There is a marked difference in adult size of the two sexes: 21 Mississippi males range from 62-84 mm (average, 73.6) in snout-to-vent length; 29 Mississippi females range from 73-92.5 mm (average, 82.3).

Habits and habitat.—Allen's (1932: 9) account of *Rana aesopus* in Harrison County, Mississippi, was based entirely upon observations of *Rana sevos*a. Practically all extant specimens of *sevos*a were collected by Morrow J. Allen, Stewart Springer, or their associates, in southern Mississippi. Neither they nor any other collectors have secured either *capito* or *areolata*, as now restricted, in this area. Furthermore, Allen states that he deposited specimens of each species in the American Museum of Natural History, and eleven Biloxi specimens of "*Rana areolata*," from that institution, have been examined by us and are here listed as paratypes of *sevos*a. Allen's account is quoted in full: "This species has been abundantly found throughout the months of October, November, and December in the burrows made by *Gopherus polyphemus*. When the temperature rises, these frogs become active and may be seen sitting in the openings of the tunnels down which they disappear at the least indication of danger. In colder weather they are never at the surface and can only be taken by digging to the bottom of the gopher hole, where never more than one is found in company of one or two turtles. The only specimen taken near the coast was found in a pool of water on January 25, 1931. Ten or twenty miles inland gopher holes are numerous and it is in this region that this frog has been found in quantity."

Fortunately, while this description was in course of preparation, Stewart Springer visited Pittsburgh and contributed additional information upon the habits of *sevos*a from memory. He recalled finding these frogs breeding in the water in southern Mississippi concurrently with *Hyla gratiosa* and *Hyla cinerea cinerea*; Allen (*supra cit.*: 8) reports the former breeding near Biloxi on April 18 and 19, and the latter "as soon as the weather becomes warm and settled." Mr. Springer further reported that the eggs, in masses about the size of two fists, are laid under water at a depth of approximately

one foot and are attached to plant stems. He stated that *sevosa* is less restricted to cypress swamps for breeding sites than is *gratiosa*, since the former occurs also in pine barren ponds, even those of temporary character. The call, as he remembered it, is less snore-like than is that of *capito*. He found that frightened individuals dive and swim along the bottom of the pond.

DISCUSSION OF THE *RANA AREOLATA* GROUP

COMMENTS UPON THE MEASURING OF FROGS

At the beginning of this study we decided to test the validity of certain measurements that are frequently made on frogs by measuring our series independently and comparing our results. Measurements are usually made to prove that individual animals differ from others of their kind in actual size; that body proportions depend upon age and/or sex; and that size ranges and growth ratios vary in different populations (ecologic, geographic, subspecific, specific, etc.). Published tabulations are frequently accepted as accurate merely because the component figures have been carried to several decimal places, because some mathematical device or formula has been used, or because the columns of figures appear too formidable for analysis. The following appear to be the chief variables that affect the accuracy of frog measurements: (1) the use of different techniques, instruments, and standards by different workers; (2) the factor of personal bias even in those rare instances in which the same methods of mensuration are used; and (3) the condition of the preserved specimens. The first variable can be eliminated entirely by establishing standard practices; the second can be discounted by measuring test series and determining the percentage of error due to personal bias; and the third, which cannot be avoided in all studies, can be eliminated from statistical studies by the use of fresh, uniformly preserved material. In our investigation we used the same instruments and agreed upon a definite method of taking each measurement, as detailed below. We determined our personal errors in mensuration, and upon this basis we recommend dropping from current usage those frog measurements in which the differences resulting from personal bias approach the magnitude of the actual size variations in the specimens. In this descriptive study we were obliged to use specimens that ranged in condition from flabby to well preserved.

Snout-to-vent length.—Previous tests have convinced the junior author

that the average worker can measure snout-to-vent length with more consistent accuracy than snout-to-coccyx length, at least in frogs of the genus *Rana*. In smaller frogs of certain genera the latter measurement may be preferable. The decision as to which of these measurements should be used in a particular group should be left to the individual monographer, but it is incumbent upon all writers to indicate which measurement is taken. In measuring snout-to-vent length, we placed each frog upon its belly on the table with its head to the left; exerted pressure with the fingers to flatten any unusual sacral curvature, and tightened vernier calipers until the righthand point touched, but did not compress, the tissue surrounding the vent. Readings were taken to the nearest half millimeter. In this method our individual readings did not differ more than one millimeter in 95 per cent of the test series, and the maximum divergence was two millimeters.

Head length.—Herpetologists measure the head length of frogs in three fashions: (1) snout to the posterior border of the tympanum; (2) snout to articulation of the skull with the vertebral column; and (3) snout to the angle of the jaws. The first method should not be used with frogs which have sexually dimorphic tympana, but in others it is a rapid and accurate measurement. We measured the distance on the left side of the head from the center of the snout to the posterior edge of the tympanic membrane, exercising care to avoid pressing the caliper point into the snout. In 80 per cent of our test series the readings agreed exactly or differed by one-half millimeter; in the remainder the difference did not exceed one millimeter.

Head width.—This measurement can be taken in two ways: by passing the calipers, held vertically, back over the head to the exact angles of the jaws; or by holding the calipers horizontally and sliding the arms back along the upper lips to the same point (in the *areolata* group specifically to the crease marking the beginning of the postlabial fold). The latter method is more accurate in forms with lateral vocal sacs, since in male frogs the anterior folds of these sacs may prevent closing vertically placed calipers to the exact head width. In 25 of a test series of 27 specimens our figures agreed to one-half millimeter or less; they differed by one millimeter in two instances.

Tibia (= tibio-fibula) length.—The measurement of the distance from the convex surface of the “knee” to the convex surface of the “heel,” with both tibia and tarsus flexed, proved slightly more variable than the preceding measurements but it is sufficiently accurate for routine taxonomic studies. In 70 per cent of the test series our figures agreed to one-half millimeter or less; in the remainder, usually to one millimeter.

Fourth toe length.—This measurement is far less accurate than any of the preceding and should be attempted only in forms that display wide variation in this character. If the toe is measured from the tip to the distal side of the subarticular tubercle, two variables are present: uniform flattening and straightening of the toe is difficult; and the tubercle, which is attached to loose skin, may slide several millimeters in either direction as the measurement is taken.

Interolecranal extent.—The distance between the elbows when the humeri are extended at right angles to the long axis of the body is affected by preservation, by the position in which the frog is held when the measurement is taken, and by the amount of tension exerted to bring the humeri to right angles. We have found that if this measurement is taken with the frog held ventral side uppermost, the resulting figure is always considerably lower than that obtained when the measurement is taken from the dorsal side. The arms of a specimen may be broken very easily in attempting this measurement.

Intergeneral extent.—The distance between the knees when the femora are extended at right angles to the body may be measured by different persons with reasonable consistency if the frog is placed belly downwards and its legs are pressed against the table and into a right angle position. It cannot be taken accurately upon large frogs held in the hand. Furthermore, specimens preserved with the hindlegs extended cannot be used for an accurate intergeneral measurement.

Conclusion.—We believe that in routine studies of moderate-sized frogs (50-100 mm), by workers using the same techniques but differently preserved material, snout-to-vent length, head length, head width, and tibia length are the only measurements that can be taken with sufficient accuracy to be worth tabulating or publishing. A single worker using uniform material may be justified in making other measurements. Two investigators, using exactly the same methods, should be able to measure distances of over 50 mm in frogs with an individual error of about 2 per cent when using miscellaneous specimens and about 1 per cent when using uniformly preserved material. Features less than 10 millimeters in size are rarely worth measuring in frogs of this group, since the errors in mensuration often exceed the individual variation that occurs in specimens of comparable size. Comparison of various small features in the same specimen by means of general statements, such as "tympanum one-half diameter of eye" is preferable to using measurements with large inherent errors.

KEY TO THE FORMS OF THE *RANA AREOLATA* GROUP

1. Chin and throat thickly spotted; belly spotted or unspotted; dorsal spots irregular in shape and without distinct light borders; head relatively broad, width of head in snout-to-vent length 2.1—2.6 times. 2
 Chin and throat unspotted except at sides; belly immaculate; dorsal spots rounded and encircled with light borders; head relatively narrow, width in snout-to-vent length 2.6—3.1 times. 3
2. Head triangular in outline; dorsolateral folds high and relatively narrow; dorsum with numerous prominent warts; dorsal spots poorly differentiated from gray, brown, or black ground color; venter always spotted at least from chin to midbody; dark bars on hindlegs separated by interspaces that are never wider than the bars. *Rana sevosia*, sp. nov.
 Head subtriangular in outline; dorsolateral folds low and very broad; dorsum smooth or lightly warty; dorsal spots distinct against pale ground color; chin and throat spotted; belly usually immaculate posteriorly; dark bars on hindlegs separated by light interspaces that are wider than the bars. *Rana capito* Le Conte
3. Head U-shaped in outline when viewed from above; dorsum often smooth, or nearly so; tibia length less than 40 mm in adults; post-tympanic fold poorly developed; dorsolateral folds narrow or only slightly raised, or both. *Rana areolata areolata* Baird and Girard
 Head orbiculate in outline when viewed from above; dorsum rugose; tibia length more than 40 mm in adults; post-tympanic fold well developed; dorsolateral folds prominent. *Rana areolata circulosa* Rice and Davis

COMPARISON OF THE SPECIES

Size.—The largest of the forms is *a. circulosa* in which males reach 108 mm in snout-to-vent length (our measurement) and females, 113 mm (Wright and Wright, 1933: 150). The largest of 6 Oklahoma males of *a. areolata* was 87 mm in length and the single Oklahoma female was 91 mm long. The largest male *sevosia* among 22 specimens was 84 mm long, and the largest of 29 females was 92.5. Wright and Wright (1933: 148) give 101 and 108 mm as the maximum size of male and female *capito*. On the basis of maximum size attained the forms may be arranged in descending order as follows:

a. circulosa—*capito*—*sevosia*—[?]*a. areolata*

Body form.—The form with the stoutest body and largest limbs is *a. circulosa*. In general proportions *a. areolata* and *sevosia* are quite similar; both have rounded bodies that are broadest about midway between the fore and hind limbs, and both have moderately heavy limbs. In contrast, *capito* is broadest in the pectoral region and tapers rapidly to a distinct "Gibson Girl" waist. From a rounded body to a triangular body the order is:

a. circulosa—*a. areolata*—*sevosia*—*capito*

Actual head shape.—The shape of the head when viewed from above is

orbiculate in *a. circulosa*, U-shaped in *a. areolata*, triangular in *sevosa*, and subtriangular in *capito*. The general head shape is affected by the length of the snout anterior to the orbits, as well as by the relative breadth and width of the head. *R. capito* has the broadest head in proportion to body length and also has the longest snout, but the tip of the snout is obtusely rounded; *sevosa* stands next in relative head width and in snout length, but its snout is acute rather than obtuse as in *capito*; both races of *areolata* have short snouts, but specimens of typical *areolata* have relatively narrower heads than specimens of *circulosa* and they differ further in exhibiting but little increase in head width posterior to the rear corner of the eye. From a relatively short to a relatively long snout the order of arrangement is:

a. circulosa———*a. areolata*———*sevosa*———*capito*

Ratio of head width in snout-to-vent length.—Both visual observations and measurements indicate that the ratio of head width to body length differs in each species, although Burt (1938: 349) denies that any significant difference in head width occurs between *areolata* and *capito*. This ratio ranges from 2.2-2.3 (average, 2.3-) in 7 *capito*; from 2.1-2.6 (average, 2.4) in 51 *sevosa*; and from 2.6-3.1 (average, 2.9) in 24 *areolata*. No intra-specific trend in proportionate head width is to be expected in stenotopic *sevosa*. Such a trend may be demonstrable in *capito* when series from the extremes of its range are available for comparison. A geographic gradient occurs in eurytopic *areolata*; 7 Indiana males of *a. circulosa* have ratios of 2.6-3.0 (average, 2.8), while 6 Oklahoma males of *a. areolata* have 2.7-3.1 (average, 2.9). From a relatively narrow to a relatively broad head the order of arrangement is:

a. areolata———*a. circulosa*———*sevosa*———*capito*

Ratio of head length in snout-to-vent length.—Measurements confirm the easily observed fact that both *sevosa* and *capito* have longer heads in proportion to body length than *areolata*. The head length enters the snout-to-vent length in 7 *capito* 2.6-2.7 times (average, 2.7-); in 51 *sevosa* 2.5-3.0 times (average, 2.8); and in 24 *areolata* (both races) 2.8-3.3 (average, 3.1). The *areolata* ratios suggest that on the average *a. circulosa* has a relatively shorter head than *a. areolata*, but much larger series are necessary to establish this gradient. From a relatively short head to a relatively long head the order is:

a. circulosa———[?]*a. areolata*———*sevosa*———*capito*

Actual tibia length.—The length of the tibia is a useful character in separating the two races of *areolata*; in 8 specimens of *a. areolata* the tibia

length ranges from 33 to 38.5 mm while in 17 *a. circulosa* the range is from 40.5 mm to 50.5 mm. The length of the tibia in *sevosa* and *capito* seems closer to that of *a. areolata* but in both species the actual length of the tibia is sometimes more than 40 mm; the largest *capito* we have seen has a tibia length of 41.5 mm and the largest *sevosa* 43.5 mm. There is some indication that Coastal Plain *a. circulosa* have slightly shorter tibiae than Central Lowland specimens, but larger series are necessary to establish this gradient.

Ratio of tibia length in snout-to-vent length.—In 24 specimens of *areolata* the tibia length is contained in the snout-to-vent length from 1.7-2.5 times (average, 2.1); in 7 *capito* the range is from 2.0-2.2 (average, 2.1); and in 51 *sevosa* the range is from 1.9-2.3 (average, 2.1). The *areolata* ratios are so variable that no generalization regarding subspecific variation in relative tibia length can be made until much larger series have been measured.

Finger length.—The three species of the *areolata* group do not exhibit any extra-specific variation in relative lengths of the fingers. The third finger is invariably the longest, but it projects beyond the tip of the next longest finger (usually the first, rarely the fourth) by only the length of its short terminal phalanx. The remaining three fingers are of very nearly equal length, but the first is generally slightly longer than the fourth, which in turn is slightly longer than the second. Thus, in 77 specimens of the group, the formula in order of decreasing length was 3-1-4-2 in 63, 3-1-2-4 in 12, and 3-4-2-1 in 2. The observed variations are not significant in view of the close similarity in actual length of fingers 1, 2, and 4.

Toe length.—In relative lengths of toes there is more variation between individuals than between the species. From 2 to 2.5 phalanges of the fourth toe project beyond the tip of the third; the latter is variable in length, ranging from much longer than the fifth (occasionally) to slightly longer (usually) or shorter (rarely). The second and first toes are much shorter than the other toes and exhibit little variation in relative length. The toe formula was 4-3-5-2-1 in 80 specimens and 4-5-3-2-1 in 2.

Webbing.—Intra-specific variations in extent of webbing exhibited by frogs of the *areolata* group are of three kinds: (1) subspecific, (2) sexual, (3) individual. Subspecific variations in the species *areolata* indicate a geographical gradient in foot character similar to that which occurs in the *Rana pipiens* group and in certain other eastern frogs. Specimens of *a. circulosa* have large feet with toes that are broad, blunt, and capable of wide spread. Specimens of *a. areolata*, however, have much smaller feet with narrower and less blunt (but not pointed) toes which cannot be

spread so widely. The total amount of web is much greater in *circulosa*, and the broad portion of the web tends to extend a little farther on the fourth toe in this race. Males of both races of *areolata* and males of *sevosa* have slightly greater palmation than do females. The same condition may occur in *capito*, although the nature of our specimens prevents a definite statement. There is some individual variation in the extent of webbing in all three species; part of this may be the result of differences in preservation. It should be noted also that many of the extant specimens of *sevosa* were kept alive for some time after collection and many have the tips of the toes badly abraded. Nonetheless, one well-preserved male of *sevosa* has the web broadly attached at the penultimate articulation of the fourth toe, although the normal condition is attachment a little beyond the antepenultimate articulation.

In foot and toe characters and in amount of webbing *sevosa* is extremely similar to *a. areolata*. In both the feet are of moderate size, the toes are of moderate width, and the web is broadly attached at or beyond the antepenultimate articulation of the fourth toe and extends as a narrow margin to the ultimate articulation. In *a. areolata* the marginal web is usually quite narrow back to its junction with the broad web, but in *sevosa* the marginal portion gradually increases in width proximally so that it forms a small triangle on either side of the antepenultimate phalanx of the fourth toe. Of the four forms *capito* has the smallest feet. Its toes are narrow and definitely pointed, the broad portion of the web does not quite reach the antepenultimate articulation of the fourth toe, and the marginal portion extending to the penultimate or ultimate articulation is quite narrow. From greatest to least amount of webbing the order is:

a. circulosa———*sevosa*———*a. areolata*———*capito*

Vomerine separation.—Each species has two short, more or less oblique series of vomerine teeth situated close together between the choanae. These are widely separated anteriorly and vary posteriorly from contact to slight separation (permitting insertion of a knife blade) or wide separation (permitting passage of a paper clip). Tabulation in these three categories indicates that there is a greater tendency toward fusion of the vomerine patches in *areolata* than in *capito* or *sevosa*. Thus, of 22 *areolata*, the vomerines were in contact in 6, slightly separated in 14, and well separated in 2; of 9 *capito* the vomerines were slightly separated in 4, and well separated in 5; of 51 *sevosa* the vomerines were slightly separated in 10, and widely separated in 41. Our figures fail to indicate a trend in vomerine separation within the species *areolata*, but they permit arrange-

ment of the three species in order from closely placed to well-separated vomerines, as follows:

areolata———*capito*———*sevosa*

Glandular folds.—The dorsolateral folds are least prominent and narrowest in *a. areolata*, in which they appear to originate at the rear of the upper eyelids, to broaden slightly above the tympana, and to extend backwards to the groin as narrow, slightly raised folds. In *a. circulosa* the folds originate on the upper eyelids, become very broad above the tympana where strong post-tympanic folds branch downward, and then extend backward as narrow, well-elevated folds to the groin. In *sevosa* the folds diverge from a common point of origin near the nostrils; pass over the upper eyelids, forming a depressed triangle on the top of the head between their inner margins; curve outward above the tympana; and extend backward as well-elevated folds of uniform and moderate width to the sacral region or slightly beyond; a more or less interrupted post-tympanic fold occurs in most specimens. In *capito* the folds follow the same course as in *sevosa*, but they are not nearly so distinct anteriorly, and posterior to the upper eyelids they become low, very broad folds which extend to, or almost to, the groin; no distinct post-tympanic fold is evident in the specimens which we have examined. *R. sevosa* has the shortest dorsolateral folds and longest and best defined postlabial folds; *a. circulosa* has the best developed post-tympanic folds; and *capito* has the broadest dorsolateral folds. From narrow to broad dorsolateral folds the order of arrangement is:

a. areolata———*a. circulosa*———*sevosa*———*capito*

Coloration and markings.—Of the three species *Rana sevosa* has the darkest dorsal coloration and the least amount of contrast between ground color and dorsal spots. Many of the paratypes are uniform black above, a condition that appears to be more characteristic of males than of females. The lightest specimens have a gray or brown ground color and dorsal spots that range from red brown to dark brown but are not black. The dorsal color and pattern are continued over the folds, which are never distinctively colored. The preserved specimens offer no indication that yellow was present on any part of the body in life. Metachrosis has not been reported in this species but may be expected to occur within a narrow color range.

R. capito has the lightest ground color, varying from creamy white to dark brown through various shades of yellow or purple; the dorsal spots are dark brown or black (Dickerson, 1908: 195). Males frequently have bright yellow dorsolateral folds, and the same color may occur on the warts.

along the upper jaw, and in the axillae and groin. Wright (1932: 338) states that color change in this species is not so rapid as in tree frogs, and he questions whether an individual frog in its normal environment would change from nearly black to white, as reported by Dickerson. The light coloration of *capito* is responsible for the vernacular name "White Frog" which is used in some parts of its range. When examined under very low magnification, most *sevosa* and *capito* display innumerable, minute pale gray or whitish spines over the entire dorsal surface, as illustrated in pl. XII, fig. 2.

The dorsal coloring and pattern of *areolata* vary individually, seasonally, and subspecifically. Color change within a period of a few hours has not been reported in this species, although Wright and Wright (1933: 151) state "When plowed out in early spring they [*circulosa*] are so dark as to be almost blackish" and "When cold and wet the frogs were very dark." The brown or black dorsal spots are variable in number and size; they are sharper edged and more nearly circular than in the other species and are usually distinctly bordered with yellowish, whitish, or cream color. The dorsolateral folds, the groin, and the concealed portions of the limbs are frequently yellow or greenish yellow in males. On the basis of preserved material and published descriptions it appears that *circulosa* has dorsal spots that are larger, darker, more constant in number, and more broadly light-bordered than *areolata*. Some *circulosa* are among the most marked North American *Ranas*, but even in our limited series considerable variation in amount of contrast between spots and ground color is evident. Until adequate series of fresh specimens of the two forms permit a careful appraisal of the extent of pattern variation in each subspecies, the identification of single, preserved specimens on the basis of pattern alone is inadvisable.

Although the appearance of the frogs is profoundly affected by metamorphosis and by amount of contrast between spots and ground color it is possible to arrange the forms in a linear sequence on the basis of ground color alone; from light to dark ground color the order is:

capito———*a. areolata*———*a. circulosa*———*sevosa*

In ventral pattern *capito* is the most variable; *sevosa* is less variable; and *areolata* is surprisingly constant, with the two subspecies failing to exhibit any differentiation in this character. All specimens of *capito* have more or less separated vermiculations of brown or black on the chin and throat. In some the spotted area includes the anterior half of the belly as well, and occasionally (probably in males only) almost the entire

venter is spotted. In *sevosa* the entire anterior half of the lower surface is thickly covered with spots and dusky markings; in males the remainder of the lower surface, except for a small pubic area, is spotted, whereas in females the central lower thigh surfaces and the posterior portion of the belly are usually immaculate. Ventral markings in *areolata* are restricted to a few spots along the mandibles and to small concentrations anterior to, or between, the fore limbs; the latter spots may almost form a narrow bridge across the pectoral region. The concealed surfaces of the hindlegs are invariably spotted in *sevosa*—more heavily in males than in females; *capito* has the concealed surfaces entirely immaculate or spotted laterally; and *areolata* always has the concealed surfaces immaculate. From an immaculate to a heavily spotted venter the order of arrangement is:

areolata———*capito*———*sevosa*

Secondary sexual characters.—Adult males of the three species of this group agree in having slightly enlarged forearms, a gray nuptial pad on the inner side of the inner finger (frequently blotched with dark in *circulosa*) and lateral vocal pouches. In each form the maximum size is attained by females. The forms differ in sexual dichromatism and in the size and distinctness of the vocal sacs. Male *capito* often have the dorso-lateral folds, warts, axillae, and groin marked with yellow; some yellow or greenish yellow is evident in certain males of both races of *areolata*; *sevosa* males generally tend to be darker and more heavily marked than females, but there is no evidence that yellow enters into the coloration of either sex. The external vocal sacs of *capito* begin at the posterior angle of the jaws and extend as plated folds of skin above the arms to or beyond the axillae. In life the vocal pouches of *capito* may inflate almost as far back as the groin. Wright (1932: 340) says, "It constitutes the most striking development in vocal sacs I have seen in North American Saliencia." The external vocal sacs of *sevosa* are similar in position to those of *capito* but they are not distinctively colored and hence are less prominent in preserved specimens than those of the other forms. The sacs in *a. areolata* are gray or gray-spotted ovals of loose skin extending from the angle of the jaw to above the forearm in preserved material. The vocal pouches of *a. circulosa* are similar in position and color but much larger. Published descriptions of calling males indicate that the sacs of *circulosa* are reniform or sausage-shaped when inflated and approximately the size of the frog's head. The size and shape of the inflated pouches of *a. areolata* or *sevosa* cannot be inferred from the appearance of the sacs in preserved specimens. In order of prominence, from small and indistinct to large and very dis-

tinct vocal sacs, preserved specimens of the forms may be arranged as follows:

sevosa———*capito*———*a. areolata*———*a. circulosa*

COMPARATIVE LIFE HISTORIES

The published references that can be allocated to *a. areolata* alone contain no life history data. Information upon the life history given in general discussions of the species *areolata* most probably refers solely to *a. circulosa*.

Breeding season.—*Rana a. circulosa* has been reported as breeding in March and April, and Smith (1934: 479) says it may breed in May. The breeding season of *capito*, as would be expected, extends over a greater period of time. The earliest breeding date on record is February 26 (Carr, 1940b: 55), and the latest is November 3 (Carr, 1940a: 64). The latter date is probably a "calling" rather than a "breeding date" for neither Carr, nor any other writer, offers evidence that *capito* lays eggs later than June. As reported elsewhere in this paper *sevosa* has been found breeding, in the Biloxi region, in mid-April.

Voice.—The voice of *circulosa* has been variously described: Gloyd (1928: 118) says that the call is as deep as that of *catesbeiana* but with more carrying power and less resonance; Thompson (1915: 6) states that it is a loud trill, hoarser than the call of *pipiens* and higher than that of *catesbeiana*; and Smith (1934: 479) reports that the call carries a mile or so. All writers agree that the call of *capito* is best described as a snore or snore-like groan. The voice of *sevosa* is of the same type as that of *capito*, but it is less like a snore.

Eggs.—Smith (1934: 479) states that the eggs of *areolata* [*circulosa*] are laid in large plinth-like masses that are five or six inches in diameter and about one and one-half inches thick; the masses are attached to the stems of plants and contain about 7000 eggs. In describing a clutch of *capito* eggs Wright (1932: 344) says: "A large mass was attached to a sedge stem. Its top was level with the surface of the water. The water was 9 inches deep. The mass was 4 x 5 inches square and 1½ inches thick. At first the mass impressed all of us as bluish. . . . The whole mass when turned over reveals the same white mass impression *R. sphenoccephala* and *R. pipiens* egg masses give." Other masses have been reported which varied from 4 x 5 x 1 inches to 12 x 4 x 2 inches in dimensions. "They may be attached to grass, sedges, pickerel weed, or other aquatic plant stems, twigs and brush or be free at times on the bottom. . . ." (Wright, 1932:

344). The eggs of *sevosa* are deposited in masses about the size of two fists and are attached to plant stems about a foot below the surface of the water.

Larvae.—The tadpoles of *sevosa* and *areolata* are unknown; that of *circulosa* has been collected but not described; and the tadpole of *capito* has been described in detail by Wright (1929: 29-30; 1932: 345-6). Wright (1932: 347) reports that some captive *capito* tadpoles transformed on August 27 and 28. No other dates of metamorphosis have been reported, but Wright (*loc. cit.*) states that the tadpoles probably transform from August to October 1, and measure from 27 to 35 or 36 mm at transformation. Wright and Wright (1933: 151) state that *areolata* [*circulosa*] metamorphoses during the first week in July at a size of 30 mm. Transformation has not been observed in *sevosa*.

Growth.—Nothing is known of the growth of *sevosa*, *areolata*, or *circulosa*. Wright (1932: 349) gives the age groups of *capito* as "28-38(?) mm at transformation; 38 (?) -52 mm first-year-olds; 52-65 mm for 2-year-olds; 66-77 mm 3-year-olds; 78-88 mm 4-year-olds; 89-102 mm 5-year-olds; 102-108 mm, 6-year-olds." Age groups should be defined on the basis of large series from a single locality; and since the above computations were obviously based upon relatively small series from various localities little reliance can be placed upon them.

Food.—*Rana a. circulosa* has been reported to feed upon beetles, spiders, crickets, ants, and crayfish (Smith, 1934: 480). Dickerson (1908: 196) and other authors have called attention to the batrachophagous proclivities of *capito*, and have described the manner in which this frog ejects the toad mucus. The species feeds upon beetles, hemiptera, and grasshoppers (Carr, 1940a: 64); birds (Dickerson, *loc. cit.*); and earthworms (Deckert, 1920: 6), as well. The mouth of *sevosa* is almost as large as that of *capito* and this species probably has similar feeding habits, preying largely upon toads and insects.

Habitat.—Crayfish holes are the preferred habitat of *circulosa* but the species has been taken under logs, in mammal holes, holes in road-side banks, and in sewers. Wright (1932: 336) states that *capito* "seems to be restricted almost solely to the burrows of the Gopher Turtle," but it can and does, live in other situations. Carr (1940a: 63) reports it in burrows of *Peromyscus polionotus*, crayfish burrows, and post holes. Furthermore, the species has been reported in Beaufort County, North Carolina, by Brandt (1936: 220) and since this locality is not within the range of *Gopherus polyphemus* other hiding places than turtle holes must be selected here. Allen (1932: 9) records *sevosa* taken from burrows of the

gopher tortoise but he does not state whether it is restricted to such burrows.

Odor.—Dickerson (1906: 195) reports that *capito* produces an offensive odor when disturbed, but such defensive behavior has not been mentioned for the other forms.

DISTRIBUTION

Rana areolata areolata occurs from Matagorda County, Texas, north to McCurtain County, Oklahoma, and Lafayette County, Arkansas; and it probably occurs in extreme northwestern Louisiana also. *R. a. circulosa* ranges from Rogers and Tulsa counties, Oklahoma, north through eastern Kansas, eastward across central Missouri and Illinois to Benton and Monroe counties, Indiana (possibly to Greene County, Ohio), and southward in the Mississippi Valley through western Tennessee to Pontotoc County,

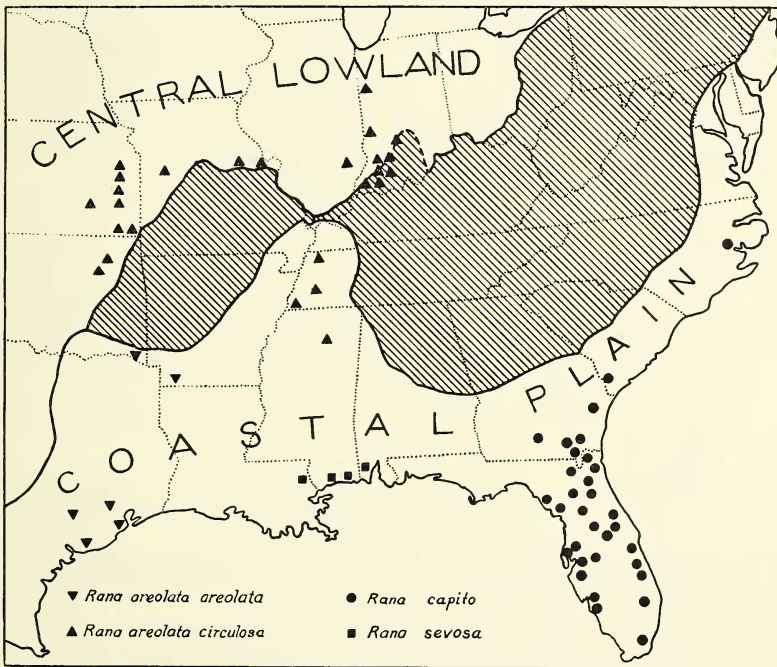


FIG. 1. Map of the distribution of the *Rana areolata* group, based upon county records as listed in this paper. Upland areas hatched.

Since the above map was prepared we have examined four specimens of *R. a. circulosa*, from Paducah, Kentucky.

Mississippi. The known range of *sevosa* extends along the Gulf coast from St. Tammany Parish, Louisiana, to Mobile County, Alabama. *R. capito* ranges from Beaufort County, North Carolina, south to Dade County, Florida, and westward to Berrien County, Georgia, and Dixie County, Florida. The easternmost station for *sevosa* is three hundred miles west of the westernmost *capito* locality; the ranges of *sevosa* and *areolata* are separated by about two hundred miles.

The frogs of the *areolata* group are lowland forms widely distributed in the Coastal Plain and Central Lowland provinces, as illustrated on the accompanying map (fig. 1). Certain *circulosa* stations in southern Indiana lie south of the plateau-lowland boundary as it is tentatively located on physiographic maps. A detailed distributional study of *circulosa* in Indiana should indicate whether or not this race has penetrated the plateau country. It appears to be significant, however, that records for all members of the group fall outside of the upland boundary except in the one region where this boundary is poorly delimited.

The following list is not a complete tabulation of museum specimens² but a list of those that we have examined. We have included the first published record for each county, also. Records that may be incorrect are preceded by a question mark and followed by discussion.

Rana areolata areolata

ARKANSAS:

Lafayette Co., KU 9278; Smith, 1934: 481

?*Lawrence Co.* A misquotation by Black and Dellinger (1938: 20) who state: "Taylor (1935) has reported one specimen from Lewisville, Lawrence County." Smith (*supra cit.*) and Taylor (1935: 210) both list Kansas University 9278 with the data "Lewisville, Lafayette County."

LOUISIANA:

"northwest." Viosca, 1931: 7

?NEW MEXICO:

USNM 3302 from "the Rio San Pedro of the Gila" (Baird and Girard, 1852: 173) was mentioned in the original description of *areolata*. It was later listed as *berlandieri* by Yarrow (1883: 180) and as *brachycephala* by Cope (1889: 405). USNM 3382 from the "St. Francisco Mountains, N. Mex." was listed by Yarrow (*op. cit.*: 178) as *Rana areolata areolata*.

² AMNH, American Museum of Natural History; CA, Chicago Academy of Sciences; CM, Carnegie Museum; FMNH, Field Museum of Natural History; KU, University of Kansas; MCZ, Museum of Comparative Zoölogy; MZUM, University of Michigan Museum of Zoology; MVP, private collection of Malcolm V. Parker; TZS, Toledo Zoological Society; USNM, United States National Museum.

Both of these specimens were most probably *pipiens* but this assumption cannot be confirmed since Dr. Cochran has informed us that the specimens have been missing from the USNM collection for many years.

OKLAHOMA:

McCurtain Co. CM 18662-68

TEXAS:

Colorado Co. Burt and Burt, 1929: 6

Galveston Co. Dickerson, 1906: 193

Harris Co. Wright and Wright, 1938: 25

Matagorda Co. USNM 3304 (type of *areolata*); Baird and Girard, 1852: 173
(original description of *areolata*)

Rana areolata circulosa

ILLINOIS:

"northern." USNM 9386

Richland Co. USNM 13828, 49590; Cope, 1889: 415

INDIANA:

Benton Co. CA 160 (type of *circulosa*); Davis and Rice, 1883: 22

Daviess Co. Swanson, 1939: 688

Du Bois Co. Swanson, 1939: 688

Martin Co. Swanson, 1939: 688

Monroe Co. Wright and Myers, 1927: 173

Pike Co. CM 13371-75; Swanson, 1939: 688

Vandenburg Co. CM 13378; Swanson, 1939: 688

Vigo Co. Blatchley, 1900: 543

Warrick Co. Swanson, 1939: 688

KANSAS:

Allen Co. Smith, 1934: 482

Anderson Co. Smith, 1934: 482

Cherokee Co. Smith, 1934: 482

Douglas Co. Hartman, 1907: 228

Franklin Co. CM 9889-90; USNM 89031; Gloyd, 1928: 117

Greenwood Co. Smith, 1934: 482

Labette Co. USNM 90318-19; Smith, 1934: 482

KENTUCKY,

McCracken Co. TZS 707-710

LOUISIANA:

?*Tangipahoa Parish.* FMNH 11980-81 (unquestionably *circulosa*) were received from the General Biological Supply House with "Louisiana" as the only original data. At our request, D. Dwight Davis of Field Museum, communicated with the donor in 1939 and received supplementary data for these specimens as follows: "Tangipahoa Parish; Ponchatoula, Martin Bankston, 1931." We question the correctness of this locality, since Tangipahoa Parish adjoins St. Tammany, where *sevosa* occurs; and since Viosca (1931: 7), on the basis of wide local experience, restricts *areolata* to northwest Louisiana.

MISSISSIPPI:

Pontotoc Co. USNM 99359; Burt, 1938: 349

MISSOURI:

Johnson Co. Hurter, 1911: 116

Montgomery Co. USNM 48697-98, 38358, 57844-48; Hurter, 1911: 116

St. Charles Co. CA 4757 and 5094

?OHIO:

Greene Co. Wright and Wright (1933: 150) list Ohio in the range of *areolata*. Dr. Charles F. Walker informs us that tadpoles hatched from eggs collected by an Antioch College student at a fish hatchery near Yellow Springs were sent to Dr. Wright and identified by him as *areolata*. Until adult *areolata* are collected in the region we feel that it is inadvisable to accept this record, especially in view of the fact that the tadpole of *areolata* has never been described. Even if adults are secured the possibility that they may have been accidentally introduced at the hatchery must be considered.

OKLAHOMA:

Rogers Co. USNM 94247; Harper, 1935: 79

Tulsa Co. Force, 1930: 27

TENNESSEE:

Obion Co. Parker, 1939: 79

Shelby Co. MVP 2827-28, 2884; Parker, 1939: 79

Rana capito

FLORIDA:

Alachua Co. USNM 4743 (type of *aesopus*); Cope, 1886: 517-518 (original description of *aesopus*)

Baker Co. Wright, 1932: 334

Brevard Co. CM 3233-34

Charlotte Co. Carr, 1940a: 63

Clay Co. Burt, 1938: 350

Dade Co. Burt, 1938: 350

Dixie Co. Carr, 1940a: 63

Duval Co. Deckert, 1914a: 3

Hillsborough Co. Loennberg, 1894: 339

Indian River Co. Wright, 1932: 348

Lake Co. Wright, 1932: 348

Lee Co. Carr, 1940a: 63

Levy Co. USNM 57533-35, 57658; Wright, 1932: 348

Manatee Co. CM 16547

Marion Co. USNM 61062; CM 9832-34; CA 21741-43; Wright, 1932: 348

Nassau Co. Wright, 1932: 348

Orange Co. Loennberg, 1894: 339

Palm Beach Co. Boulenger, 1920: 467

Pasco Co. Harper, 1935: 80

Pinellas Co. Dickerson, 1906: 194

- Polk Co.* USNM 50576, 59413; MVP 42; Boulenger, 1920: 467
Putnam Co. USNM 20513-14, 21702-04; Boulenger, 1920: 467
St. Lucie Co. Burt, 1938: 350
Seminole Co. Fletcher, 1900: 47
Volusia Co. Wright, 1932: 348

GEORGIA:

- Berrien Co.* USNM 11897; Cope, 1889: 412
Branley Co. Wright, 1932: 334
Charlton Co. Wright, 1932: 334
 ?*Fulton Co.* Burt (1938: 350) lists this county from "literature" but we have not been able to locate any such record. The occurrence in this region of a species that is coastal plain in distribution is highly improbable.
Liberty Co. USNM 5903 (type of *capito*); Le Conte, 1855: 425 (original description of *capito*)
Ware Co. Wright, 1932: 334

NORTH CAROLINA:

- Beaufort Co.* Brandt, 1936: 220

SOUTH CAROLINA:

- ?*Hampton Co.* Deckert (1920: 26) states that he received a specimen from "near Pinelands, Hampton Co." This locality does not occur on any maps examined by us.
Jasper Co. Chamberlain (1939: 28) suggests that Deckert's specimen may have come from Pineland, Jasper County. The two counties are contiguous and an error in county location may easily have been made.

Rana sevosa

ALABAMA:

- Mobile Co.* Löding, 1922: 20

LOUISIANA:

- Saint Tammany Parish.* CM 16809 (type of *sevosa*)

MISSISSIPPI:

- Harrison Co.* CM 4944, 18116-17, 18184-97; FMNH 11511-14; MCZ 15803-06; MZUM 76921, 71777; Allen, 1932: 9
Jackson Co. AMNH A37089-99; CM 5407-08; FMNH 21610

ORIGIN AND EVOLUTION OF THE *RANA AREOLATA* GROUP

Previous writers have failed to agree upon the affinities of *areolata* and *capito*. Cope (1889: 409) writes of *areolata* (including *capito*): "This well-marked species is related to the *R. palustris*, but is easily distinguished." Dickerson (1906: 194) states that *aesopus* agrees with *palustris* and *pipiens* in color and markings, but that it is very distinct from them in general appearance. Wright (1932: 351) says, "Our second consideration that *R. aesopus* is closely related to *R. pipiens* and *R. sphenoccephala* does not mili-

tate against some relationship with *R. palustris* but *R. palustris* is not the nearest relative." Boulenger (1920: 418) groups *pretiosa*, *cantibrigensis*, *sylvatica*, *godmani*, and *areolata* (including *capito*) together on the basis of the outer metatarsi being bound together in their basal portions.

All too little attention has been devoted to the elucidation of primitive and specialized characters in North American frogs. Writing of *Rana* Boulenger (1920: 418) says, "I conceive the most primitive type as with large nasal bones in contact with each other and with the fronto-parietals entirely covering the ethmoid; pointed, fully webbed toes with the outer metatarsals separated by web to the base; a distinct tympanum; no glandular dorso-lateral fold." Toe character and amount of palmation are so subject to geographic variation that they must be used with extreme care in phylogenetic inquiries. The members of the *areolata* group agree in having small, well-separated nasals, fronto-parietals that leave the ethmoid largely exposed, well-developed folds, and outer metatarsals partly joined. In these characters they are specialized, if Boulenger's ideas are accepted; the distinct tympanum is the only supposedly primitive character retained by the group.

Since the *areolata* group appears to have had a southwestern center of origin, we have examined the principal reports upon Mexican frogs in searching, unsuccessfully, for a possible ancestral stock. Two names, discussed below, have been applied to Mexican frogs that resemble *areolata* (judging from published descriptions and figures only) in several respects. While it is geographically improbable that any actual relationships are involved the similarities are worth mentioning.

Rana forreri Boulenger³ was based upon a female from Sinaloa which was subsequently figured by Günther.⁴ Later Boulenger (1920: 430) himself referred *forreri* to the synonymy of *halecina* (= *pipiens*), and Kellogg⁵ concurred in this disposition of the form. Surprisingly Günther's figure of transmontane *forreri* bears a remarkable resemblance to certain cismontane *areolata*. For example, CM 18666, from Oklahoma, differs in having a slightly more triangular head, a few more dorsal spots, interbars between the dark bars on the hind legs, and slightly less webbing. The fact that some Mexican *pipiens* agree with certain *areolata* in dorsal pattern may indicate an ancestral connection between the two forms that provided potentialities for similar pattern development, but it must not be taken

³ 1883. Ann. & Mag. Nat. Hist., (5), 11: 343

⁴ 1900. Biologia Centrali-Americana, Reptilia and Batrachia, pl. 60, fig. A.

⁵ 1932. Bull. U. S. Nat. Mus., no. 160: 203

to mean that a Sinaloa *pipiens* population was involved in the ancestry of *areolata*.

Rana montezumae Baird was based upon specimens from the City of Mexico and upland specimens correctly referred to this form are certainly not close to *areolata*. At various times, however, specimens have been referred to *montezumae* which are certainly not conspecific and which in some cases, at least, merit re-examination in the light of possible affinities with *areolata*. For example, Baird (1859, pl. 36, fig. 1-6) illustrates two very different frogs, unfortunately without locality data, as *montezumae*. Fig. 5 is referred to as a young specimen, but it is obviously a breeding male of a frog similar to *areolata*. Furthermore its vomerines, as shown in Fig. 6, are strikingly different from those of the "adult" *montezumae* shown in Fig. 3. We suggest that museum series of *montezumae* should be rechecked, and that specimens which resemble Baird's Fig. 5 merit comparison with *areolata*.

Similarities in life history, vocal equipment, pattern, and general structure offer a preponderant weight of evidence that the *Rana areolata* group developed from a *pipiens*, or a *pipiens*-like, stock by reduction in amount of webbing, increase in glandular folding, slight multiplication of dorsal spots, and increase in size of vocal sacs. Confirmatory evidence is offered by Cope (1889: 410) who states, "As a whole, the *Rana areolata* is pretty well distinguished by its very short palmation. Nevertheless, I have seen a specimen from Guatemala with similar posterior feet, which is otherwise not different from the *R. virescens*."

Although the affinities of the group as a whole may be open to question, we believe that the trend lines listed above present definite indication of the evolution of the forms in the group. Since *circulosa* is only subspecifically distinct from typical *areolata* it may reasonably be considered to be a fairly modern race that evolved in the Central Lowlands, and then extended its range southward in the Mississippi Valley in post-glacial times. Boulenger's (1883: 16) synonymizing of *circulosa* with *septentrionalis* was the result of his having received Canadian frogs that had been erroneously identified as *circulosa*. Later (1920: 430) he transferred *circulosa* to the synonymy of *areolata*. Examination of a larger series of specimens enables us to restore it to subspecific rank.

At any time from the upper Miocene on, the stem stock of *areolata* could have migrated eastward along the Gulf Coastal Plain, its route being either north or south of the present coastline, depending upon the date of the migration. This eastward movement probably antedated the for-

mation of the present Mississippi delta and may well have occurred in the late Pliocene. All morphological evidence indicates that *sevosa* and *capito* arose from a common ancestral stock; that neither one can have been directly derived from the other; and that they are more closely related to each other than either is to *areolata*. The development of the modern Mississippi River may conceivably have served as the barrier that isolated the eastern population from its Texas progenitor and permitted differentiation toward the gopher-frog type. At some later date a barrier developed somewhere between the Apalachicola River in Florida and Mobile Bay; it effectively divided the gopher-frog stock and led to the differentiation of *sevosa* and *capito*. What this barrier may have been can only be conjectured, but we venture to suggest that it may have been an early interglacial (first?) increase in sea level,⁶ which submerged most of peninsular Florida except for a few islands, produced the Brandywine Terrace (270 feet above present sea level), submerged the entire Apalachicola River, and embayed its western fork, the Chattahoochee. *R. sevosa* apparently developed in a humid region, and *R. capito* in a more arid environment. The hypothesis of the evolution of the former *in situ* in Mississippi swamps and of the latter on a relatively small island in the region of north-central Florida is in accord with the present environments of the two forms. A salt-water barrier may not have been required for the isolation of the Mississippi and Florida populations, however; at the present time, with no such barrier intervening, the ranges of *sevosa* and *capito* are well separated. Further study of the zoögeography of the Gulf coast will probably serve to emphasize the faunal dissimilarities of Florida and Mississippi. Many forms that are thought to have continuous ranges from Florida to New Orleans may be expected to exhibit discontinuities between the Apalachicola River and Mobile Bay. The present barrier in this region may be climatic, but its exact location and character must await detailed studies of many species. It is suggestive that the westernmost Florida record for *Gopherus polyphemus* listed by Carr (1940a: 105) is Liberty County, which has the Apalachicola as its western boundary. The gopher turtle occurs commonly west of Mobile Bay, but we do not know of any definite records from southeastern Alabama. If, on further study, the range of this turtle proves to be discontinuous, it will afford an interesting parallel to the *sevosa-capito* distribution. Its absence in an area must not, however, be considered a barrier to gopher frog occupancy; for, since Harper's statement (1935: 81)

⁶ See Cooke (1939, Florida Geol. Bull. no 17, fig. 12-16) for illustrations of Pleistocene shore lines in the southeast.

that the range of *capito* lies wholly within that of *G. polyphemus*, *capito* has been reported from Beaufort County, North Carolina (Brandt, 1936: 220), and *polyphemus* is not known to occur north of the Aiken region of South Carolina.

Our conclusions as to the phylogeny of the *areolata* group are expressed graphically below.

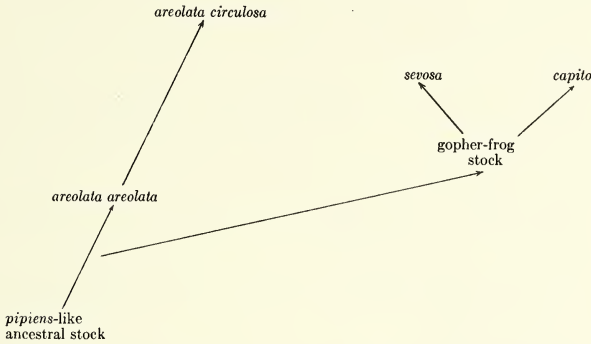


FIG. 2. Diagram of the probable relationships of the forms of the *Rana areolata* group.

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EXPLANATION OF PLATE XII.

MISS OLIVE BEAN, del.

- FIG. 1. Adult male *Rana sevos*a, sp. nov., drawn from preserved specimens. Natural size.
- FIG. 2. A portion of the dorsum of *Rana sevos*a, sp. nov., to show folds and warts; drawn from an enlarged photograph of a preserved specimen. About twice natural size.